ON *SPELAEOGRIPHUS*, A NEW CAVERNICOLOUS CRUSTACEAN FROM SOUTH AFRICA

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SYNOPSIS

A new cavernicolous Malacostracan from a pool in a cave on Table Mountain, *Spelaeogriphus lepidops* n.g. and sp., is described and figured. The affinities of the genus are discussed. In some respects it resembles *Monodella* (Thermosbaenacea), in others it approaches the Anaspidacea (Syncarida), or the Tanaidacea (Peracarida), but it is not referable to any of these Orders. Specimens received later included an ovigerous female carrying ten to twelve large ova in a characteristic Peracaridan brood-pouch composed of five pairs of oostegites. The genus, therefore, belongs to the Division Peracarida and, as it is not referable to any of the existing Orders of that Division, is placed in a new Order Spelaeogriphacea and a new family Spelaeogriphidae each with the characters of the genus. Nothing is known of the internal anatomy or of the embryology.

INTRODUCTION

Recently members of the South African Spelaeological Association obtained some specimens of a small blind Malacostracan from a pool at a depth of 110 ft. in a cave on Table Mountain, South Africa. The animals were said to " swim swiftly with rapid undulations of the body ". The temperature of the water in which they lived was 50° F. (February, 1956).

The specimens were submitted to Dr. K. H. Barnard who found that they represented a new genus and species of Crustacea Malacostraca which at first sight seemed referable to the Division Syncarida but on closer examination seemed rather to belong to the Peracarida—its " affinities seem to be with the Tanaidacea, especially *Apseudes* " to quote from Dr. Barnard's letter. In April 1956 Barnard sent to the British Museum six of the specimens, together with notes and sketches, and suggested that I might like to describe this interesting new species and discuss its affinities in more detail. I wish to express my thanks to Dr. Barnard for presenting these specimens to the Museum and also for the privilege of studying them.

The specimens were sent to London in two small vials. One vial contained two almost-perfect specimens which are quite opaque and much better preserved than the other four ; these have been selected as the holotype, a male measuring 7·2 mm. in length (from tip of rostrum to posterior margin of telson) and the allotype, a female measuring 5·6 mm., respectively. The four paratypes are very delicate, almost transparent, and more or less imperfect as to their appendages ; they range from 4·9 to 6·8 mm. in length and comprise two females and two males (one rather immature). The holotype and allotype have been handled with care and, for the

necessary dissection, the more incomplete paratypes have been used. Some specimens have been retained for the South African Museum collection and according to Barnard the largest measures 7·5 mm. in length.

The name suggested by Barnard for this new genus was most appropriate but, unfortunately, it is now preoccupied by *Spelaeocaris* Matjašič (1956, p. 65) a new genus of the family Atyidae. I therefore propose the name *Spelaeogriphus* from " griphos " meaning something complicated, a puzzle or riddle, not " gryphos " meaning a griffin (Jaeger, 1955).

Spelaeogriphus n. g.

Diagnosis. Body elongated, subcylindrical (somewhat depressed). Carapace short, deep, coalescing dorsally with first thoracic somite and overhanging on each side to largely conceal the mouthparts and to enclose a branchial cavity within which lies the large, pedunculate, cup-like epipodite of the first thoracic limb (maxilliped). Each lateral flap of carapace deeply separated anteriorly from the dorsal part ; cervical furrow visible in the better-preserved specimens. Thoracic somites 2–8 free (although the second is almost entirely overlapped by the carapace), deepening progressively posteriorly. Abdomen long, exceeding half the total length of body ; telson distinct from the last somite. Ocular lobe oval, plate-like, movably articulated to side of rostrum, without visual elements or pigment. Antennulae almost contiguous basally, long, with two unequal or subequal flagella and a 3-segmented protopodite without statocyst but modified in the adult male. Antenna longer and more robust than antennula ; protopodite 2-segmented (peduncle therefore 4-segmented), exopodite small, scale-like, multiarticulate flagellum nearly as long as body. Mandible with lacinia mobilis, a series of 16–20 spines and a slender, 1-segmented palp. Maxillula with a slender palp near distal end of outer margin of endite 3 (broad outer lobe). Maxilla well developed ; endite 3 deeply bifurcate, each lobe with long curved apical setae ; a few stout penicillate processes on endite 2 (inner lobe). Maxilliped " Isopodan " in form, with a few retinacula on inner margin of inner plate (endite of basipodite) a 5-segmented palp, no exopodite, a large respiratory cup-like epipodite. Lower lip without movably articulated apical lappets. Peraeopods simple, ambulatory, none markedly modified ; epipodites absent ; exopodites present on 1–6 (a rudiment on 7 is exceptional). Three anterior pairs of exopodites 2 (3)-segmented, setose, natatory ; three posterior pairs 1 (2)-segmented, non-setose, respiratory (gills). Pleopods alike in both sexes ; first four pairs well-developed, biramous, natatory, fifth pair vestigial. Uropods broad, biramous ; exopodite 2-, endopodite 1-segmented. A simple penial process on coxopodite of peraeopod 7 in male ; incipient oostegites on peraeopods 2–5 in female (not mature). In a more mature female sent after this paper was completed oostegites are present on peraeopods 1–5 inclusive (see p. 44).

Nothing is known of the internal anatomy or of the development.

Gender of genus : masculine. Genotype : *Spelaeogriphus lepidops* n. sp.

Holotype, allotype and the paratypes described below will be incorporated in the British Museum Collection.

Spelaeogriphus lepidops n. sp.

DESCRIPTION. The slender elongate *body* recalls that of many small cavernicolous Malacostraca ; it is subcylindrical being slightly depressed especially in the posterior third. In dorsal aspect the sides are almost parallel throughout, except posteriorly since the free telson is narrower than the abdominal and thoracic somites. In lateral aspect the body is as represented in Text-fig. 1 but the delicate side plates (pleura or epimera) of abdominal somites 1–4 are not at first glance apparent and therefore these somites appear to be less deep.

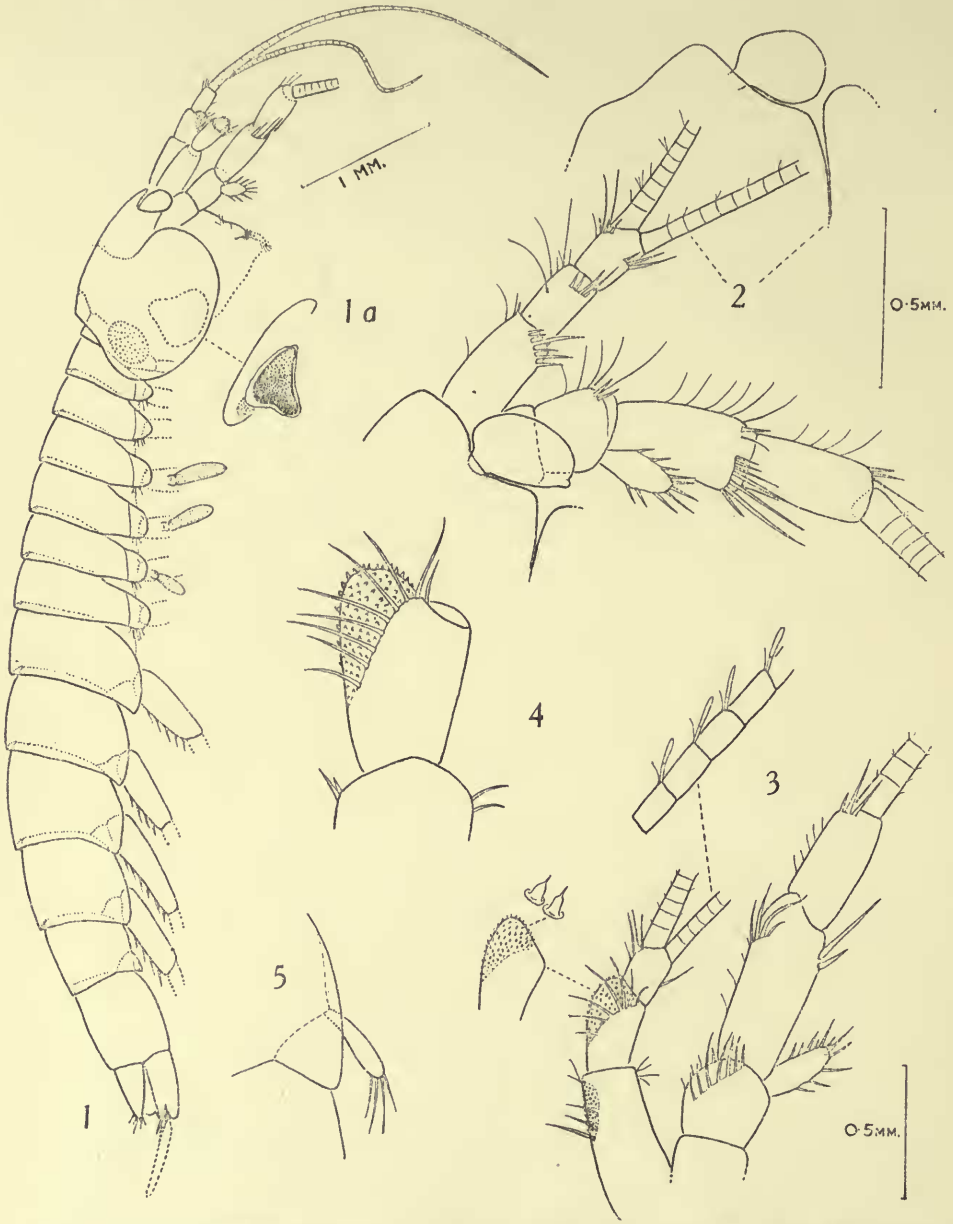
The small, distinct *carapace* is smooth except for the cervical furrow which is distinct in the holotype, but only faintly indicated in the more transparent specimens. It is produced anteriorly, between the pair of oval ocular lobes or scales, to form a somewhat depressed, broadly triangular rostrum (Text-fig. 2). In lateral aspect, the carapace is as deep as long and, in all the preserved specimens (which may be somewhat contracted), it overlaps the first free thoracic somite (number 2) leaving only a small portion exposed dorsally, and part of the third somite laterally (Text-fig. 1). Each lateral part of the anterior margin of the carapace is continued backwards, on a level with the outer rim of the ocular scale, for a considerable distance before fusing with the dorsal portion at the cervical furrow. Thus these antero-lateral flaps are doubtless capable of considerable lateral movement. Near the postero-lateral margin there is a conspicuous oval patch, above thoracic somite 2, represented by stippling in Text-fig. 1. This area, whose significance is unknown, is part of the carapace wall and can also be seen from the inside, as shown in Text-fig. 1*a*, where the ventral rim of the carapace is indicated, slightly posterior to the respiratory cup-like epipodite of the maxilliped. This large " gill " is visible through the thin wall of the carapace, but the oval patch behind it is not equally well marked in all the specimens ; for example, it is rather faint in the immature male paratype.

Thorax. The first somite is completely fused with the head region ; the second somite is free from, but almost entirely overlapped by, the carapace. Somites 3–8 become progressively deeper as represented in Text-fig. 1 although their dorsal margins are approximately equal in length.

The *abdomen* exceeds half the total length of the body. Somites 1, 2 and 5 are subequal in length and shorter than the remaining three. Somites 1–4 decrease gradually in depth but, as already mentioned, their pleura are delicate and not easy to discern. The small epimeral portion of somite 5, however, is distinct (Text-fig. 1).

The *telson* is free from, and narrower than, the sixth abdominal somite (Text-fig. 1*b*). The median length is nearly equal to the basal width and the rounded apex bears a number of spines of varying length.

The *antennulae*, which are not widely separated from each other, are shorter and much less robust than the antennae. The proximal part of the right antennula of a female paratype is represented, in dorsal aspect, in Text-fig. 2, that of the holotype in latero-ventral aspect, in Text-fig. 3. The first segment of the protopodite, which is equal to the sum of the second and third segments, has no statocyst. In the adult male the second segment of the peduncle is modified, the distal half of the inner margin being expanded to form a lobe which is richly beset with rows of



FIGS. 1–5.—*Spelaeogriphus lepidops* n.g. and sp. Fig. 1. ♂ paratype, in lateral aspect, peraeopods omitted except for the exopodites or " gills " on 4–6 respectively. 1*a*. Ventral margin of carapace and cup-like epipodite at base of the maxilliped. Fig. 2. Lower figure—rostrum, right ocular lobe and proximal segments of antennula and antenna of a ♀ paratype, in dorsal aspect ; upper figure—rostrum and right ocular lobe of the smallest paratype, an immature ♂, in dorsal aspect. Fig. 3. Proximal segments of antennula and antenna of the holotype, in ventro-lateral aspect (the segments of the protopodite are broader than shown in figure) and, at higher magnification, a few distal

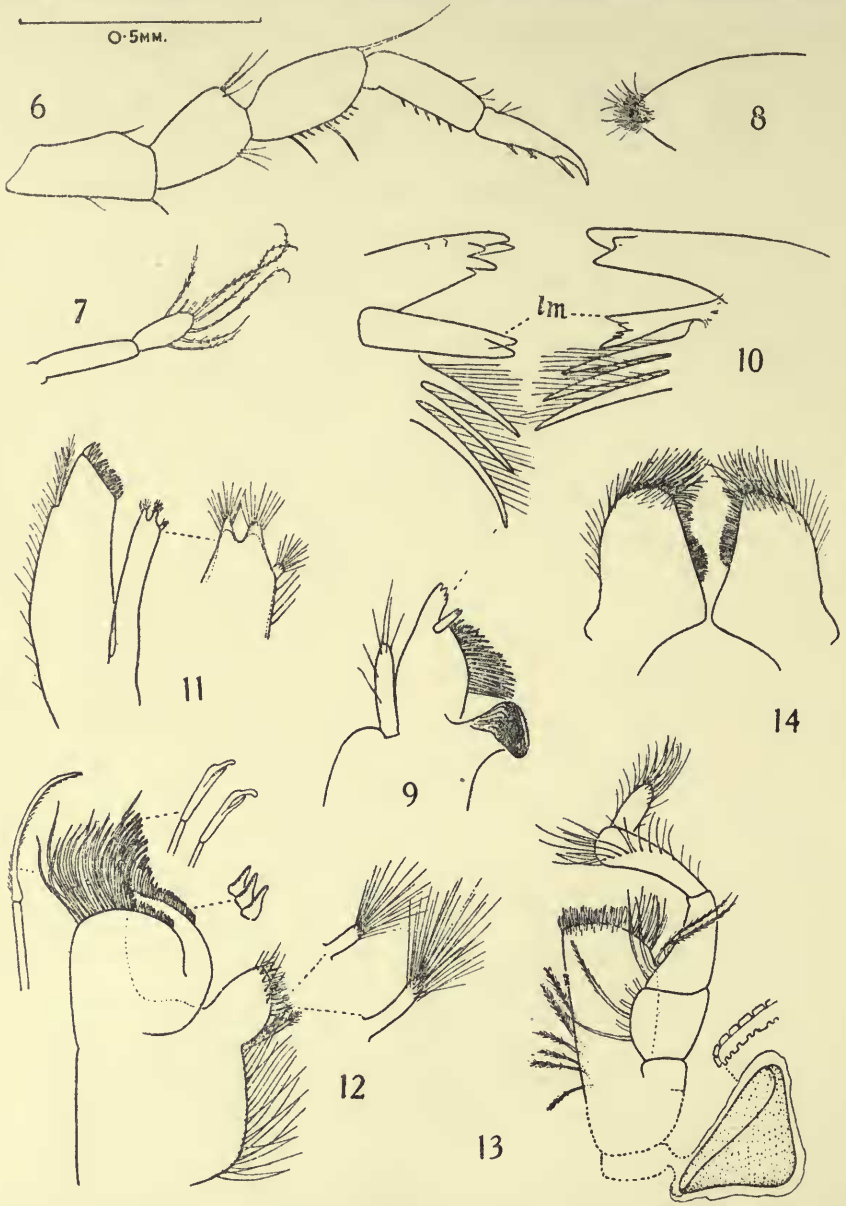
conical papillae. Ventrally, this lobe is bounded by a series of long setae as shown in Text-figs. 3 and 4. There is also a small patch of the special, sharply pointed, conical papillae on the inner distal margin of the basal segment of the male peduncle. The longer flagellum comprises 40 or more segments, the smaller up to 36 segments ; in some specimens the two flagella are nearly equal in length. The distal three-fourths of the shorter (outer) flagellum has a series of short aesthetascs as shown in the enlarged portion (Text-fig. 3).

The *antennal* peduncle of a female is represented in dorsal aspect in Text-fig. 2, that of the male holotype in latero-ventral aspect and at a lower magnification, in Text-fig. 3. There is no obvious sexual dimorphism of the peduncle or protopodite. The small, scale-like exopodite bears some 10 marginal spines. The flagellum when complete is almost as long as the body and comprises about 70 segments.

The *ocular lobe* is a thin oval scale, movably articulated by means of a short peduncle to the side of the rostrum (Text-fig. 2) ; on the posterior outer edge is a tiny papilla. If viewed obliquely, the ocular scale seems to be decidedly club-shaped. There is no trace of pigment or of visual elements.

The *mouthparts* represented in Text-figs. 8–14 are, with the exception of the maxilliped (Text-fig. 13), all from the same female paratype. The upper lip, as indicated in Text-fig. 1, is deep ; the distal portion is represented in lateral aspect in Text-fig. 8. The distal portion of the left *mandible* is shown (slightly distorted by pressure of the coverslip of the micropreparation) in Text-fig. 9. The palp is reduced to one elongate segment, the molar process is well developed and the spine row comprises 16–20 graded spines. There is only very slight asymmetry of incisor process and lacinia mobilis respectively (Text-fig. 10). The robust outer lobe (endite 3) of the *maxillula* bears about 16 short apical spines and, on the distal outer margin, a slender plumose seta-like palp (Text-fig. 11) ; the rather slender inner lobe (endite 1) has three short plumose terminal papillae. The *maxilla*, together with various details at a larger magnification, is represented in Text-fig. 12 ; endite 3 is deeply bifurcate, the long curved spines on the outer lobe consist of a shaft and a slightly curved distal portion whereas those of the inner lobe have the apex bifurcate. The short inner spines of each series are somewhat conical with striate or serrulate concave (? outer) margins. Endite 2 has a few stout penicillate setae, three short and one long, on the inner margin. The *maxilliped* represented in Text-fig. 13 is from a considerably smaller specimen and, as it was not completely removed, the proximal portion (indicated by a broken line in the figure) may not be quite exact although the relative size and position of the epipodite is correct, the concavity facing inwards and forwards. The two maxillipeds are held firmly together by means of a few small retinacula on the inner margin of the inner plate (endite of the basipodite). The palp appears to be 5-segmented; the wide second segment bears 6 stout plumose setae on the inner margin ; the third segment, which

segments of the shorter antennular flagellum. Fig. 4. Second segment of antennular protopodite of ♂ paratype, in ventral aspect, to show specifically modified area beset with rows of conical papillae. Fig. 5. Vestigial pleopod 5 of ♂ paratype, highly magnified. Scale of Fig. 1 and 1*a* = 1 mm. Scale of Figs. 2 (lower) and 3 respectively = 0·5 mm.



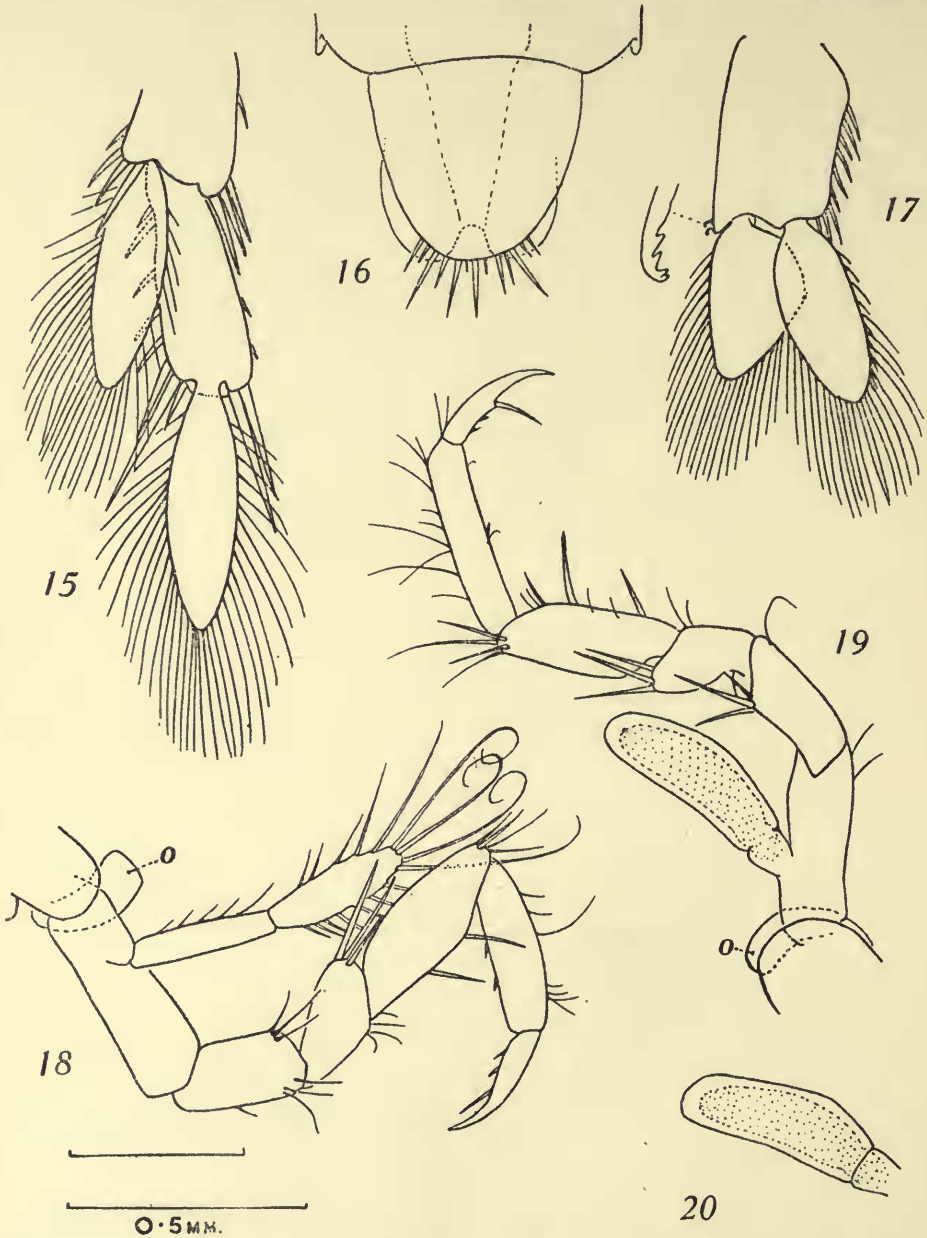
FIGS. 6–14. *Spelaeogriphus lepidops* n.g. and sp. ♀ paratypes. Fig. 6. Distal segments of peraeopod 1. Fig. 7. Exopodite of peraeopod 1 of a larger specimen. Fig. 8. Upper lip, in lateral aspect. Fig. 9. Distal part of left mandible, slightly distorted by the coverslip of microslide. Fig. 10. Portion of left and right mandibles, at higher magnification, to show slight asymmetry of incisor process and lacinia mobilis. Fig. 11. Maxillula, and apex of inner lobe more highly magnified. Fig. 12. Maxilla, with enlarged details of setae and spines. Fig. 13. Maxilliped of a smaller specimen, in ventral aspect (appendage broke just below the palp; position of epipodite relative to the maxilliped is correct. Fig. 14. Lower lip. Figs. 8–12 and 14 from the same specimen. All except Fig. 10 drawn to scale = 0·5 mm.

is contracted distally, also has marginal plumose setae ; the fourth segment is somewhat expanded distally and the fifth is inserted at an angle to the apex. The *lower lip*, represented in Text-fig. 14, shows no trace of the movably articulated lappet on each lobe which is characteristic of the family Apseudidae.

Peraeopods. The peraeopods, which are simple and ambulatory (pediform), are arranged in two series, an anterior one of three, and a posterior one of four, pairs as shown in Dr. Barnard's sketch (Text-fig. 26). This division is emphasized by the fact that the exopodites on each of the three anterior pairs are natatory whereas those on peraeopods 4–6 respectively are reduced and modified to serve as gills (Text-figs. 1 and 18–20). In the allotype there is also a minute gill or exopodite on the right peraeopod 7, but this is exceptional. Each natatory exopodite consists of an elongate proximal, non-setose or sparsely setose, segment and a distal segment bearing marginal setae, the apical ones being especially long and often curled ; in addition a very short basal segment may be more or less clearly demarcated (Text-figs. 7, 18, 21, 24 and 25). The respiratory exopodites, the posterior of which is quite small, lack the setose terminal segment ; the proximal segment is swollen and specially modified and again there is a more or less distinct small basal segment (Text-figs. 1, 19, 20 and 22).

In the adult male peraeopods 1–3 are considerably more robust than in the female or young male, but otherwise there is no sexual dimorphism. The first peraeopod is the only one which may be regarded as slightly modified ; it is rather shorter than either peraeopod 2 or 3, with a smaller exopodite, a broader carpus, and more numerous spinules on the ventral margin of carpus and propodus respectively (Text-figs. 21 and 24). Text-figs. 24 and 25 represent peraeopods 1 and 3 respectively, drawn to the same scale, of the male paratype shown in Text-fig. 1 ; peraeopod 2 is very similar to, though a trifle shorter than, peraeopod 3. In the holotype, which is rather larger, the spine-setae on the carpus are more numerous, especially in one of the two rows (3 and 5–6, as against 2 and 2 in the paratype represented in Text-fig. 25). When the distal segments are flexed these two rows lie one on either side of the propodus. Peraeopods 4–7 are relatively more slender and increase gradually in length owing chiefly to the progressive elongation of the carpus and especially of the propodus (cf. Text-figs. 22 and 23, peraeopods 4 and 7 respectively, of a male in the South African Museum). Peraeopod 7 as a rule lacks the exopodite ; a simple penial process is present in all three males on the coxopodite. This process is short in the smaller male paratype with the as yet unmodified antennular protopodite (and therefore rather immature) ; in the adult male it is long so that the two processes almost meet in the median line (Text-fig. 23).

The peraeopod represented in Text-fig. 6 was already detached from one of the paratypes but it probably came from one of the females ; in the allotype the first peraeopod has some spinules on the ventral margin of carpus and propodus and the exopodite is shorter, especially as regards the terminal segment, than that on either peraeopod 2 or 3 (cf. Text-figs. 7 and 18). Peraeopod 4 is more slender than peraeopod 3, with a longer more slender propodus ; the exopodite shows a hint of the short basal segment which, however, is distinct in that of peraeopod 5. What I consider to be incipient oostegites are present at the bases of peraeopods 2–5 but they are



FIGS. 15–20. *Spelaeogriphus lepidops* n.g. and sp. Fig. 15. Uropod of allotype. Fig. 16. Telson and posterior margin of abdominal somite 6, in dorsal aspect. Fig. 17. Fourth pleopod, with grappling hook more highly magnified. Fig. 18. Third right peraeopod of ♀ with well developed natatory exopodite and incipient oostegite *o*. Fig. 19. Fourth peraeopod with respiratory exopodite or "gill" and oostegite. Fig. 20. Detached exopodite of peraeopod 5. Figs. 16–20 from same ♀ paratype. Figs. 15 and 17 at smaller scale = 0·5 mm.; rest at larger scale = 0·5 mm.

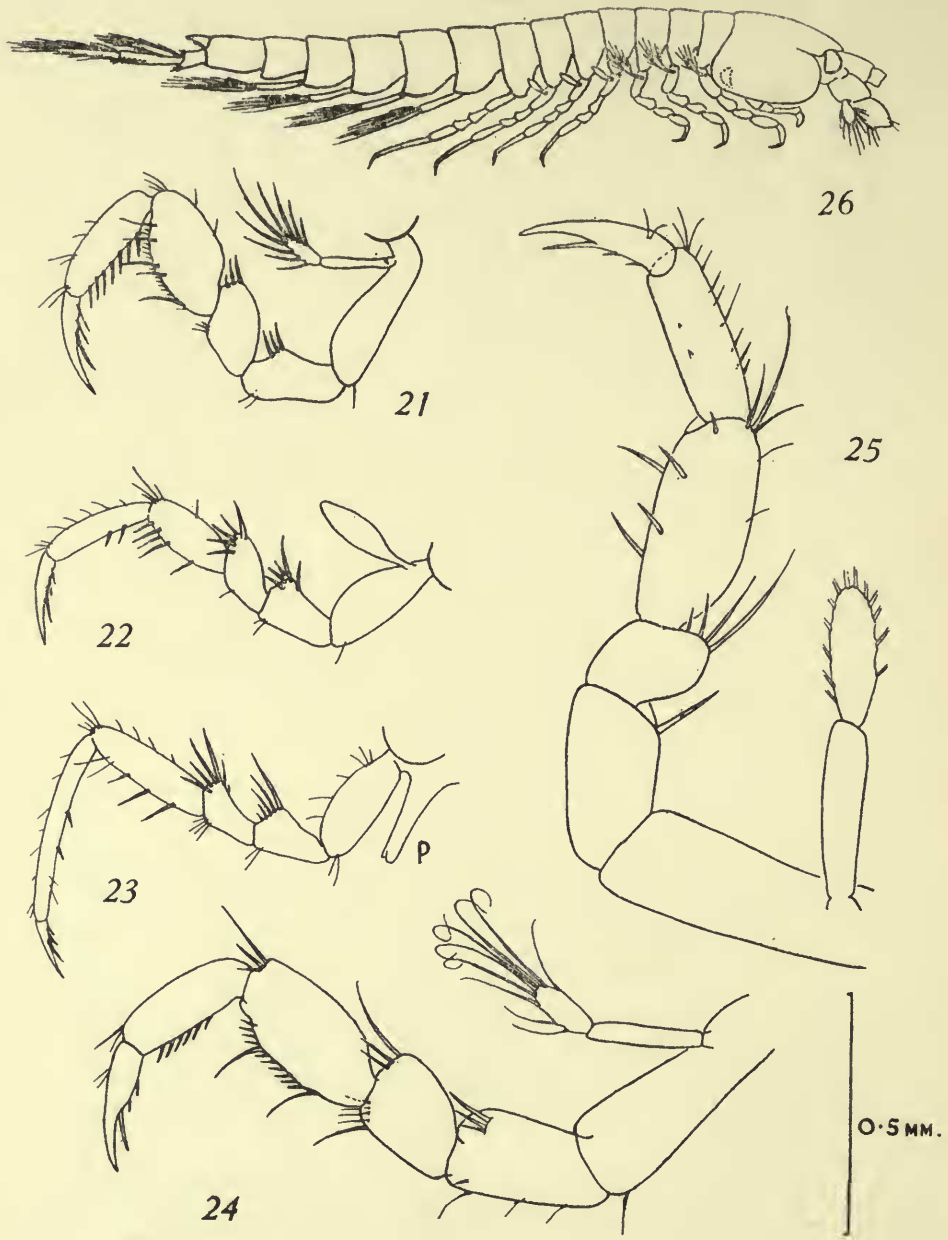
not easy to make out (Text-figs. 18 and 19, *o*). As in the male, peraeopods 5–7 lengthen progressively and the respiratory exopodite on peraeopod 6 is smaller than that on peraeopod 5. Perhaps none of the female specimens is fully mature since the oostegites are so small and inconspicuous.

Pleopods. These are alike in both sexes. The first four pairs are well developed and natatory. Each comprises a broad protopodite with two retinacula at the distal end of the inner, and a series of spines on the outer, margin and a paddle-shaped, heavily setose exopodite and endopodite (Text-fig. 17). The fifth pair is very much reduced and concealed by the small epimera of the fifth abdominal somite. In Text-fig. 5 the fifth pleopod has been displaced so that the drawing could be made, it is reduced to a slender club-shaped segment with 4 terminal setae.

The *uropods* appear to be very fragile since in none of the specimens are they now complete ; either the exopodite, or both exopodite and endopodite are as a rule missing. In the vial containing the holotype and allotype two detached but complete uropods were found. These must belong to the allotype since in the holotype the peduncles are still attached to the specimen. One of these uropods is represented in Text-fig. 15 ; the short stout protopodite is furnished with an outer and an inner cluster of apical spines ; the exopodite is 2-segmented, the proximal segment is armed with spines along the inner margin and apically—the latter spines being especially long, the distal segment is very similar in shape and size to the exopodite and both are heavily setose. In the case of the male paratype represented in Text-fig. 1 the exopodite and endopodite had apparently undergone regeneration and are smaller than is normal for the species, so in the illustration I have indicated the normal length of the endopodite by a broken line and have omitted the exopodite (which in any case is most frequently missing).

Remarks. The material available is insufficient for a study of the differences due to age and sex. Apart from that exhibited by the protopodite of the antennula (Text-figs. 2 and 3–4), sexual dimorphism appears to be slight. The segmentation of the antennular flagella is indistinct proximally, where the segments appear to be crowded, becoming more distinct distally. Dr. Barnard gives the number of segments of the flagella as about 36 and 48 respectively but this is presumably the maximum number found in the largest specimen ($l = 7{\cdot}5$ mm.). In the holotype the two flagella are not very unequal but the number of segments seems to be about 32–33 and 40–42 respectively. In the allotype the flagella are markedly unequal yet each appears to have less than 30 segments (about 24 and 28 respectively). These differences may be due to sex. In the other specimens the flagella are not always complete.

In the smallest male there is as yet no trace of the sexual modification of the first two segments of the antennular protopodite. Indeed, the antennula is relatively much shorter than in the adults, especially as regards the basal segment of the protopodite ; the smaller flagellum comprises only 15–16 segments. The larger flagellum is missing, as also are the antennae beyond the short protopodites (the two basal segments). The rostrum is also appreciably shorter than in the adults, and the ocular lobes are much more circular in outline (upper figure in Text-fig. 2).



FIGS. 21–26. *Spelaeogriphus lepidops* n.g. sp. Figs. 21, 22 and 23. Peraeopods 1, 4 and 7 respectively of a ♂ in South African Museum—sketches by Dr. K. H. Barnard; magnification not stated. Specimen probably larger than the holotype. Figs. 24 and 25. Left peraeopods 1 and 3 respectively, of ♂ paratype represented in Fig. 1. Scale = 0·5 mm. Fig. 26. Sketch of whole animal, in lateral aspect, by Dr. K. H. Barnard, showing arrangement of peraeopods in two groups, pleopods and uropod.

The first peraeopod is very similar to that of the female (Text-fig. 6) ; the others are all incomplete although in most instances the proximal segments with the well developed exopodites remain.

In a female paratype of approximately the same size as the male represented in Text-fig. 1 ($l = 6{\cdot}5$ mm.) the antennular protopodite is more slender and, especially as regards the first segment, shorter than in the male and there are fewer segments in the shorter flagellum ; the longer one is incomplete. The protopodite of the antenna is also relatively shorter and more slender (the male antennular and antennal protopodites are considerably broader than I have indicated in Text-fig. 3 where the appendages are lying obliquely, but I did not wish to risk damage to the holotype). The first three peraeopods of the male become more robust with increase in size ; in the holotype they are somewhat more robust than in the paratype from which Text-fig. 24 was obtained and Dr. Barnard's sketch is probably from a male exceeding 7 mm. in length. (Text-fig. 21).

AFFINITIES OF THE GENUS *SPELAEOGRIPHUS*

In recent years many new cavernicolous and interstitial Crustacea Malacostraca have been discovered ; these are referable for the most part to the Orders Thermosbaenacea, Bathynellacea (Syncarida), Isopoda and Amphipoda (Peracarida).

Spelaeogriphus, with its slender, elongate body, bears a striking resemblance to one of these cavernicolous forms namely, *Monodella argentarii* Stella (1951*a*, p. 2, fig. 1). But, the general similarity of telson, uropods, mandible (the palp excepted) and the exopodites[1] of the peraeopods notwithstanding, *Spelaeogriphus* is most certainly not referable to the Thermosbaenacea. This Order is unique amongst Malacostraca in the possession of a *dorsal* marsupium or brood-pouch in the female, " a chamber formed by the posterior portion of the carapace, which covers the first three somites of the body " (Stella, 1951*b*, fig. 3 of plate ; 1953, pl. 1, fig. 2). Barker exhibited some ovigerous or larvigerous females of *Thermosbaena mirabilis* Monod, with a similar dorsal marsupium, at the XIV International Congress of Zoology held in Copenhagen in 1953, but his description and figures have not so far been published (Barker, 1953). Fertilization in the Thermosbaenacea must, therefore, be internal. In *Monodella*, according to Stella (1955, p. 464), from each ovary a short duct, the vagina, leads to the base of the sixth peraeopod and another one, the oviduct, goes dorsally to the brood-pouch. The position of the vaginal openings on the seventh thoracic somite (bases of peraeopods 6) is unusual ; in Malacostraca the female genital openings are, as a general rule, on the sixth somite. Another unusual feature in *Monodella* is the presence in the male of an additional coupling organ on the maxilliped (Stella, 1955, p. 464 ; Karaman, 1953, figs. 7 and 10). These characters, together with a study of the embryology of *Monodella*, led Taramelli (1954) to exclude the Order Thermosbaenacea from the Division Peracarida and with this Siewing agrees (1956, p. 168, Diagram 3). The Thermosbaenacea have certain characters of the Syncarida, others of the Peracarida, and still others which are unique.

When Barnard first examined the specimens of *Spelaeogriphus* he thought that

[1] None of these exopodites are respiratory in *Monodella*.

they belonged to the Division Syncarida. But, he writes, " further consideration shows the impossibility of including this Crustacean in that Division. Barring a superficial resemblance in having exopods on six of the peraeopods, it has none of the special features found in the Syncarida. On the contrary, its affinities seem to be with the Tanaidacea, especially *Apseudes*. The mouthparts are Isopodan in character, and the cup-like epipod on the maxilliped is clearly analogous to that found in *Apseudes* " (Barnard, in letter received 14.iv.56). After I had described *Spelaeogriphus* and had considered its possible relationships, I sent some notes and sketches to Dr. K. Lang, Director of the Stockholm Museum, since he has for some years past been engaged on a revision of the Order Tanaidacea. He replied in the following few words : " The animal you picture does not belong to the Tanaidacea but to the Anaspidacea " (letter dated 20.vii.56). Thus two eminent authorities on the lower Eumalacostraca disagree as to the systematic position of *Spelaeogriphus*.

In my opinion *Spelaeogriphus* does not agree with either the Anaspidacea or the Tanaidacea as at present defined. In fact, like the Thermosbaenacea, it does not quite fit into either the Syncarida or the Peracarida. In Kükenthal & Krumbach's *Handbuch der Zoologie*, Zimmer (1927, p. 566) defines the Divisions of the Eumalacostraca and, as regards the external characters, *Spelaeogriphus* differs from the Syncarida and agrees with the Peracarida in having : (i) a carapace which encloses gill chambers but leaves most of the thoracic somites free ; (ii) a lacinia mobilis on the mandible ; (iii) two, not three, segments distal to the " knee " of the peraeopods ; (iv) oostegites in the female (but see later, p. 44). The antennal protopodite consists of two, not three, segments so that the peduncle comprises four segments ; this holds for some Syncarida and also (though not mentioned by Zimmer in his diagnosis on p. 566) for the Tanaidacea alone amongst the Peracarida (Calman, 1909, p. 191 ; Zimmer, 1927, p. 686). Thus there is something to be said in favour of Barnard's view that *Spelaeogriphus* is a primitive Apseudid.

On the other hand, the genus differs in quite a number of respects from Zimmer's (1927, p. 685) diagnosis of the Tanaidacea. There are seven, not six, free thoracic somites. The sides of the carapace are deep and separated anteriorly for a long distance from the dorsal or median part. The telson is distinct from, not fused with, the last abdominal somite. The abdomen itself is far longer than that of the Tanaids; but this difference may not be significant since in the Thermosbaenacea *Monodella* has a long, *Thermosbaena* a short, abdomen. The exopodites are more numerous and well developed, three pairs being natatory, three pairs respiratory ; in the Tanaidacea vestigial exopodites are sometimes present on the first two pairs of peraeopods only. While the form of the ocular lobe and of the epipodite on the maxilliped strongly recall the Apseudidae, *Spelaeogriphus* differs from that family in other respects, namely : The first peraeopods are *not* chelate or subchelate, nor is the second pair modified and fossorial. The antennulae are set closer together and are decidely smaller than the antennae. The mandibular palp is reduced to one segment, not " triarticulate " ; but this is probably of slight importance since the palp is absent in the family Tanaidae. The palp of the maxillula is *not* large and reflexed into the gill chamber, but small and placed near the distal end of endite 3 (in *Anaspides* the palp is even smaller, though more proximally placed, see

Chappuis, 1927, p. 596, fig. 584). There are no apical lappets on the lower lip. The uropods are broad, natatory whereas in Apseudids exopodite and endopodite are, as a rule, slender and multiarticulate. The Tanaidacea are entirely marine. I do not think that *Spelaeogriphus* is referable to the Order Tanaidacea, nor can it be placed in any of the other Peracaridan Orders—Cumacea, Mysidacea, Isopoda or Amphipoda.

In addition to the characters already mentioned (p. 42), *Spelaeogriphus* differs from the Anaspidacea in other respects : Epipodites are absent from all the peraeopods, whereas in Anaspidacea there are one or two on each, with the exception of the last pair. The pleopods are alike in both sexes, and the endopodite is well developed in the anterior four pairs ; in the Syncarida the endopodite is rudimentary or absent, with the exception of the first two pairs in Anaspididae and Koonungidae, in which the endopodites are modified as copulatory organs in the male (Chappuis, 1927, p. 594 ; Smith, 1909, figs 29 and 52 ; Nicholls, 1931, pl. 32, figs. 12 and 13). A thelycum or spermatheca appears to be absent in *Spelaeogriphus* but is present in Anaspidacea (Smith, 1909, fig. 27 ; Nicholls, 1931, p. 476, figs A and B). There is no statocyst in *Spelaeogriphus* such as occurs in e.g. *Koonunga* (Smith, 1909, p. 502, fig. 5). Certain characters of *Spelaeogriphus*, on the other hand, do recall those of some Anaspidacea. For example, both *Spelaeogriphus* and *Koonunga* exhibit sexual dimorphism of the antennulae although the modified area in the male differs in position and in form in the two genera (c.f. Zimmer, 1927, p. 595, fig. 580 with Text-fig. 3 of the present paper). The three pairs of respiratory exopodites on peraeopods 4 to 6 in *Spelaeogriphus* are unusual—they resemble epipodites but from their position on the limbs both Barnard and I think they must be exopodites. The only other Eumalacostraca with exopodites of this type are Syncarida ; in the Anaspididae peraeopod 6 (thoracic limb 7) bears, in addition to the two epipodites, a reduced respiratory exopodite, whereas those on the anterior peraeopods are long and multiarticulate (Smith, 1909, p. 516, fig. 24 and p. 513, fig, 21). The free second thoracic somite, free telson and broad uropod recall the Anaspidacea and in *Koonunga* there is a distinct V-shaped notch above the attachment of the antenna in the frontal margin of the cephalon (Sayce, 1908, pl. 1, figs. 1 and 3) ; in *Spelaeogriphus* there is a long slit in this position (Text-figs. 1, 2). It is possible to imagine a Syncarid *with* a carapace since, in the Division Peracarida, the carapace is present or absent and, when present, varies greatly in relative size. According to Barnard the mouthparts are Isopodan in character but the maxillula is not unlike that of Anaspidacea, especially the position and direction of the palp (Sayce, 1908, pl. 1, fig. 12 ; Smith, 1909, p. 508, figs. 13, 14). In the Anaspididae the mandible shows a hint of bifurcating although there is no lacinia mobilis, and the proximal epipodite on the maxilliped is large although not cup-like (Smith, 1909, figs. 9, 10 and 19). If *Spelaeogriphus* is a Syncarid it certainly is not referable to either the Anaspididae or the Koonungidae. Nor can it be placed with the minute rather degenerate members of the Bathynellidae although, if Uéno's observations are correct, some species of this family would seem to possess oostegites. Dr. Chappuis, whom I consulted on this point, writes " No! there is no brood pouch in *Bathynella* or *Parabathynella* ; the eggs are laid one after the other just where the animal happens

to be" (letter dated 22.v.26). Yet Miuri and Morimoto (1953, p. 239) say of *Bathynella morimotoi* Uéno " Adult females carrying eggs and newly-hatched larvae are obtainable at all seasons of the year". In the following year Uéno (1954, p. 525, fig. 3*b*) figures a long elliptical lamella on the coxopodite of the second peraeopod of *Bathynella inlandica* n. sp. and says that these structures, which are also present on the first pair of peraeopods, are presumably oostegites (marsupium). Here then is a Peracaridan character in certain species of the Bathynellacea.

Like the Thermosbaenacea, *Spelaeogriphus* possesses certain characters of the Syncarida, others of the Peracarida. For the present it seems advisable to refer it to a new family, Spelaeogriphidae, with the characters of the genus, and to leave the systematic position of the family as uncertain. Perhaps when the internal anatomy and the embryology of *Spelaeogriphus* are known the systematic position of the family will be elucidated. As new forms of primitive Eumalacostraca come to light it may be necessary to revise the classification and even to redefine the major Divisions.

ADDITIONAL NOTE

After the manuscript was finished I received from Dr. Barnard two further specimens accompanied by the following note: " New species of shrimp; pair found copulating. Bats Cave, stream at bottom. Collected by S.A.S.A. 29.7.56." The male and female were thought to be copulating when caught, and each should therefore be sexually mature. Unfortunately, uropods, antennulae and antennae are incomplete in both and in the male the posterior two or three peraeopods are broken and most of the gill-like epipodites are missing.

In the male, which measures 6·5 mm. in length, the modified lobe on segment 2 of the antennular protopodite is more pronounced distally than that represented in Text-fig. 4 and the conical papillae extend almost to the proximal articulation of the segment; the patch on the inner distal margin of segment 1 is conspicuous. There seem to be a few papillae at the inner distal angle of segment 2, and a row of 5 blunt cones on the inner margin of segment 3, of the antennal peduncle. The body of the female is slightly bent, but it appears to be rather shorter and is more slender than that of the male. The oostegites are quite unmistakable in this specimen although they are narrower than one might expect in a breeding female. In addition to the four pairs which I detected in the type specimens, a small pair is present on peraeopods 1. The first four pairs meet or even overlap medially; each member of the fifth pair is only about as long as wide and does not quite reach the median line.

In both specimens the peraeopods are rather bunched together and each is flexed towards its partner. Barnard sketches the peraeopods as arranged in two series, 1–3 directed forwards and 4–7 directed backwards (Text-fig. 26) and in life this may be the case.

There can now be no doubt as to the presence of a ventral thoracic marsupium such as is characteristic of the Division Peracarida. *Spelaeogriphus*, therefore, seems referable to that Division and, as far as the external characters are concerned, it agrees with the definition of the Peracarida given by Calman (1909, p. 149) and

also that given by Zimmer (1927, p. 566) if very slightly modified to read " . . . Antennenstamm 2- oder 3-gliederig." (As already mentioned, Zimmer failed to recall that the antennal protopodite of the Tanaidacea is only 2-segmented, although he does mention this in his treatment of the Order on p. 686). However, the family Spelaeogriphidae cannot be placed in the Order Tanaidacea for reasons which I have already given (p. 42). Nor can it be placed in any of the other Peracaridan Orders although the elongated abdomen and free telson, the large number of exopodites, and the sexual modification of the antennula in the male are characters which it shares with the Mysidacea. The only alternative, therefore, is to establish a new Order Spelaeogriphacea, with the characters of the family, to receive it.

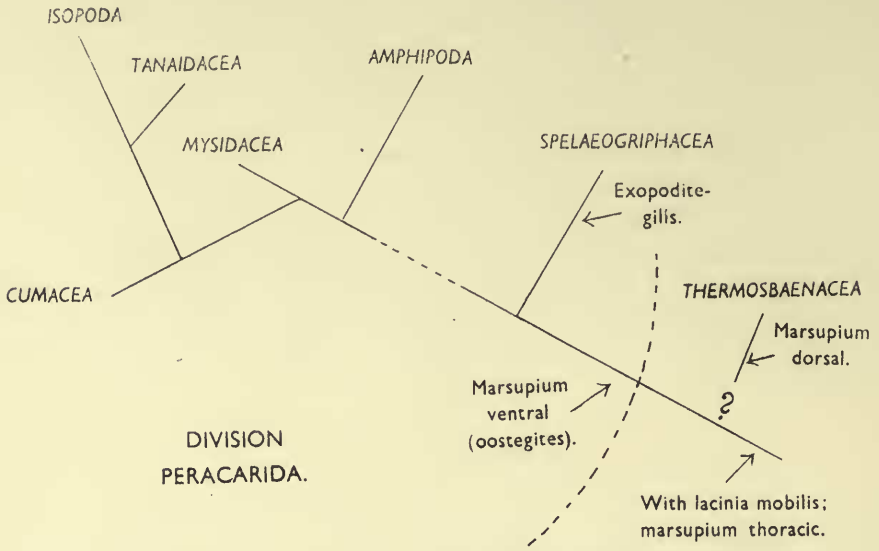
It is to be hoped that ovigerous females and larval stages may soon be collected and also that specimens fixed in Bouin or another suitable fixative will be available for sectioning.

Postscript 18.xii.56.

After the manuscript had gone to press I received five additional specimens collected in Bats Cave, on 9.ix.56 by the S.A.S.A. One of these is an ovigerous female with a relatively large brood-pouch containing about 10–12 large ova ; the outlines of the separate oostegites are not clearly distinguishable but it is a normal Peracaridan brood-pouch composed, as already stated, of five pairs of oostegites on peraeopods 1–5 (somites 2–6).

I also sent tracings of the illustrations to Dr. Rolf Siewing of Kiel, who has done some excellent work on the comparative morphology of the Crustacean Malacostraca. He replied as follows : " Mit grosser Freude habe ich Ihre Zeichnungen von *Spelaeogriphus lepidops* studiert. Der neue Fund hat mich sehr interessiert . . . Meine Meinung nun zu der Neuentdeckung ist, dass es sich nicht um einen Vertreter der Syncarida handelt. Es fehlen bei *Spelaeogriphus* Epipodite, die bei den Syncarida wenigstens an einigen Thorakalextremitäten ausgebildet sind. Ein freier Carapax ist bei den Syncarida ebenfalls niemals ausgebildet. Die Oostegite und die Lacinia mobilis sind aber ganz typische Charakteristica der Division Peracarida. Ich halte es nicht für wahrscheinlich, dass sich diesse Organe unabgehängig in einer anderen Kategorie der Malacostraca noch einmal entwickelt haben. Auffällig sind aber manche Übereinstimmungen mit den Thermosbaenacea : Bau der Extremitäten des Thorax, Carapax, und Lacininia mobilis der Mandibel. Möglicherweisse ist *Spelaeogriphus* mit ihnen näher verwandt und stellt ein primitives Bindeglied dar. Sicher wird die Untersuchung der inneren Anatomie weitere Aufschlüsse geben."

I too had been much impressed by the resemblances between *Spelaeogriphus* and *Monodella*—apart from the position of the marsupium, which is ventral in *Spelaeogriphus* and all the Peracarida, dorsal in the Thermosbaenacea. Dr. Siewing's comments have been most helpful and give me more confidence in proposing the new Order Spelaeogriphacea. The position of this primitive Peracaridan Order in Siewing's Diagram 3 (1956, p. 168) would appear to be within the Division Peracarida, near the suggested position of the Thermosbaenacea, thus :—



Adapted from Siewing, 1956, p. 168. Upper left-hand portion of Diagram 3.

The Thermosbaenacea and the Peracarida have a lacinia mobilis on the mandible and a thoracic brood-pouch or marsupium. The Spelaeogriphacea have three pairs of exopodites modified as gills ; this may be a secondary specialization, perhaps an adaption to the freshwater habitat, although no other cavernicolous Malacostracan possesses such gills. The relationship of the Spelaeogriphacea to the other Peracaridan Orders must, for the present, remain uncertain.

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